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Peanut Breeding and Genetic Resources

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I. INTRODUCTION

Peanut is widely used as an oilseed crop around the world and as a direct
source of human food in the United States. Several species of peanut
have been cultivated for their edible seeds, but only *Arachis hypogaea*
L. has been domesticated and widely distributed. Production in the
United States is completely mechanized, but in many other regions the
seeds are planted and harvested by hand. In the United States, approx-
imately 70 percent of the peanuts are runners (small-seeded types of var.
hypogaea), 20 percent are virginias (large-seeded types of var. *hypogaea*),
10 percent are spanish (var. *vulgaris*), and less than 1 percent are valen-
cia (var. *fastigiata*) market types (Knauft and Gorbet 1989). *Peruvian* and
aequatoriana types are produced in only a few countries in Central and
South America.
   In the United States, production is controlled by a federal price sup-
port system that controls the quantity and guarantees a minimum price
to the producer. Historically, it has been to the producer's advantage to
maximize yields by having large amounts of inputs during each crop
year. Thus, in the United States, plant breeders have concentrated efforts
on maximizing yields under the constraints of market acceptability.
Large amounts of pesticides are applied to the crop and in recent years,
breeding for insect and disease resistance has become a priority. In other
regions of the world, especially in drier areas, there are few inputs used
for subsistence production systems. Yields are restricted in most areas
worldwide by diseases, especially leaf spots (Shokes and Culbreath
1997) and rust (Subrahmanyam 1997), and yield per hectare averages
less than half of the United States production. Incorporating biotic stress
tolerance is an objective of breeding efforts in areas where applying
pesticides and fungicides is not economical. However, incorporating dis-
ease resistance or tolerance tends to decrease yield potential. The crop
improvement situation has dramatically changed within the past few
years in the United States as restrictions for pesticide applications have
been imposed and with the occurrence of diseases (e.g., tomato spotted
wilt virus) for which no chemical controls are available. Thus, much of
the plant breeding efforts are being redirected from only developing
cultivars with high yields to ones that are also incorporating resistance
genes to plant and seed pathogens.
   Consumer concerns about food quality of peanut has become increas-
ingly important. Because peanuts are susceptible to *Aspergillus* infec-
tion which results in aflatoxin production, all seed lots are tested at
buying points and by processors to eliminate toxins from the food chain.
Peanuts also have proteins that result in allergic reactions in about 0.6

percent of the population (Li et al. 2000). Trace amounts of peanut protein can lead to fatal anaphylactic reactions in individuals allergic to peanuts, and this is a great concern for the industry. In the United States, many peanuts are dry roasted, which apparently increases the allergic properties of the proteins (Maleki et al. 2000). Refined peanut oil does not contain protein and thus the oil is allergen free. However, when the seed is cold pressed, as is done in many parts of the world, proteins remain in the oil used for cooking and allergic reactions can occur.

There are four market types in the United States (runner, virginia, spanish, and valencia), and during the 1970s and the 1980s, three cultivars ['Florunner' (Norden et al. 1969), 'Florigiant' (Carver 1969), and 'Star' (Simpson 1972)] dominated production. The large-seeded virginia types are predominately grown in the Virginia–North Carolina area, but during the past few years there also have been significant hectarages in western Texas. The runner market type is grown predominately in the Southeast and Southwest, and spanish types are grown in Texas and Oklahoma, although their importance has greatly diminished during recent years. Valencia market types are mostly produced in New Mexico for the in-shell market, but to a lesser extent in other regions for the fresh market or boiling trade. Virginia types are consumed as in-shell or roasted products, whereas most of the runner types are used for peanut butter. In most other countries, peanuts are crushed for oil, but in the United States only seed lots deemed unsuitable for human consumption are used for oil stocks. These seed lots usually are high in aflatoxins, which are eliminated during oil extraction and purification, and there is a significant price reduction to producers.

Uniformity of commercial product has been promoted by the industry, so peanut breeding programs have selected new cultivars that closely match previous ones in size and quality traits. Cultivars that have had wide distribution are commonly used as parents in hybridization programs, and thus the genetic base of peanut cultivars has historically been very limited. However, since the late 1980s, a large number of diverse cultivars have been released by private and public plant breeding programs, and consequently the genetic base of commercially produced germplasm is much broader at the present time. Parental selection is an important consideration in plant breeding, and with uniformity requirements imposed by the peanut industry, the genetic base of peanut will continue to be relatively narrow in the future.

The genetics of peanut was reviewed by Wynne and Coffelt (1982), Murthy and Reddy (1993), and Knauft and Wynne (1995). Both qualitative and quantitative variations are abundant in the domesticated peanut, but the inheritance of only a few traits has been documented.

Reciprocal cross differences have also been reviewed by these authors for yield and other agronomic traits, which result from cytoplasmic and paternal inheritance. Because of the excellent reviews already in print about breeding methodologies for peanut, this chapter will concentrate on summarizing germplasm issues, interspecific hybridization, as well as breeding efforts with *A. hypogaea* and related species since the reviews published by Knauft and Ozias-Akins (1995) and Knauft and Wynne (1995).

II. EVOLUTION AND TAXONOMY

Species in the genus *Arachis* are distinguished from most other plants by flowering above ground, but producing fruits below the soil surface. Peanut is a member of the *Fabaceae,* tribe Aeschynomeneae, subtribe Stylosanthinae in the genus *Arachis.* Only *A. hypogaea* has been domesticated, although several species have been cultivated for their seed (*A. villosulicarpa* Hoehne and *A. stenosperma* Krapov. and W. C. Gregory) or forage (*A. pintoi* Krapov. and W. C. Gregory and *A. glabrata* Benth). The domesticated species was described by Linneaus in 1753 as *Arachis* (from the Greek "arachos," meaning weed) and *hypogaea* (meaning underground chamber).

Arachis hypogaea is believed to have originated in the southern Bolivia to northern Argentina region of South America, and in this region many types are found with primitive plant, pod, and seed characteristics. The species is an annual herb with two subspecies that are primarily distinguished by branching pattern and distribution of vegetative and reproductive nodes along the mainstem and lateral branches. Subspecies *hypogaea* has two botanical varieties (*hypogaea* and *hirsuta*), and subsp. *fastigiata* has four botanical varieties (*fastigiata, vulgaris, peruviana,* and *aequatoriana*) (Krapovickas and Gregory 1994) (Table 6.1). Isleib and Wynne (1983) grouped lines using principal component analyses and found that most morphological differences are observed between subspecies. Six *A. hypogaea* centers of diversity have evolved in South America, including the geographic regions of (1) Guarani (Paraguay-Paraná), (2) upper Amazon and west coast of Peru, (3) Goiás and Minas Gerais region of Brazil, (4) Rondonia and northwest Mato Grosso regions of Brazil, (5) southwest Amazon region in Bolivia, and (6) northeastern Brazil. An important center of diversity also exists in Africa where a large amount of variation was likely generated through hybridization and selection in different African environments (Wynne and Coffelt 1982). Although *A. hypogaea* is believed to have originated east of the Andes Mountains, the oldest archeological findings are in

Peru, dated ca. 1500 BCE (Banks 1987; Banks et al. 1993) where peanut predates the remains of maize (*Zea mays* L.) in the region of the Casma Valley. This Peruvian site may be the oldest simply because of good preservation conditions of pods in the dry climate, or there could have been a secondary domestication event; although recent molecular data indicates a single origin of *A. hypogaea* (Kochert et al. 1996).

Table 6.1. *Arachis hypogaea* subspecific and varietal classification.[a]

Botanical Variety	Market Type	Location	Traits
hypogaea		Bolivia, Amazon	No flowers on the mainstem; alternating pairs of floral and reproductive nodes on lateral branches; branches short; relatively few trichomes
	Virginia		Large seeds; less hairy
	Runner		Small seeds; less hairy
hirsuta	Peruvian runner	Peru	More hairy
fastigiata			Flowers on the mainstem; sequential pairs of floral and vegetative axes on branches
	Valencia	Brazil— Guaranian Goias Minas Gerais Paraguay Peru Uruguay	Little branched; curved branches
peruviana	Peru, N. W. Bolivia		Less hairy, deep pod reticulation
aequatoriana	Ecuador		Very hairy, deep pod reticulation; purple stems, more branched, erect
vulgaris	Spanish	Brazil— Guaranian Goias Minas Gerais Paraguay Uruguay	More branched; upright branches

[a]After Stalker and Simpson (1995).

In addition to the domesticated species, 68 wild species have been described (Krapovickas and Gregory 1994), and several additional ones have been collected but are without descriptors (Valls 2000). *Arachis* species are native to a large region of South America extending from the foothills of the Andes to the Atlantic and from the northern shores of Brazil to about 34°S in Uruguay. Valls et al. (1985) reported that species distributions are nearly continuous, and there is an extensive amount of distributional overlap among taxa in different sections of the genus.

The greatest amounts of variation are found in Brazil where species of *Arachis* originally evolved (Gregory et al. 1980). The genus has been divided into nine sections (Krapovickas and Gregory 1994) (Table 6.2), which consists of diploid ($2n = 2x = 20$), tetraploid ($2n = 4x = 40$) and

Table 6.2. Arachis species identities (type holotype unless other wise designated) (from Krapovickas and Gregory 1994; Stalker and Simpson 1995).

Section and Species	Status	Collector[d]	Collection No.
Section *Arachis*			
batizocoi Krapov. & W. C. Gregory	–	K	9505
benensis Krapov., W. C. Gregory & C. E. Simpson	*sp. nov.*	KGSPSc	35005
cardenasii Krapov. & W. C. Gregory	*sp. nov.*	KSSc	36015
correntina (Burkart) Krapov. & W. C. Gregory	*com. nov.*	Clos	5930
cruziana Krapov., W. C. Gregory & C. E. Simpson	*sp. nov.*	KSSc	36024
decora Krapov., W. C. Gregory & Valls	*sp. nov.*	VSW	9955
diogoi Hoehne	–	Diogo	317
duranensis Krapov. & W. C. Gregory	*sp. nov.*	K	8010
glandulifera Stalker	–	St	90-40
helodes Martius ex Krapov. & Rigoni	–	Manso	588
herzogii Krapov., W. C. Gregory and C. E. Simpson	*sp. nov.*	KSSc	36030
hoehnei Krapov. & W. C. Gregory	*sp. nov.*	KG	30006
hypogaea[a,b] L.	–	Linn.	9091
ipaensis Krapov. & W. C. Gregory	*sp. nov.*	KMrFr	19455
kempff-mercadoi Krapov., W. C. Gregory & C. E. Simpson	*sp. nov.*	KGPBSSc	30085
kuhlmannii Krapov. & W. C. Gregory	*sp. nov.*	KG	30034
magna Krapov., W. C. Gregory & C. E. Simpson	*sp. nov.*	KGSSc	30097

Section and Species	Status	Collector[d]	Collection No.
Section *Arachis (cont.)*			
microsperma Krapov., W. C. Gregory & Valls	*sp. nov.*	VKRSv	7681
monticola Krapov. & Rigoni	–	K	8012
palustris Krapov., W. C. Gregory & Valls	*sp. nov.*	VKRSv	6536
praecox Krapov., W. C. Gregory & Valls	*sp. nov.*	VS	6416
simpsonii Krapov. & W. C. Gregory	*sp. nov.*	KSSc	36009
stenosperma Krapov. & W. C. Gregory	*sp. nov.*	HLK	410
trinitensis Krapov. & W. C. Gregory	*sp. nov.*	Wi	866
valida Krapov. & W. C. Gregory	*sp. nov.*	KG	30011
villosa Benth.	–	Tweedi	1837
williamsii Krapov. & W. C. Gregory	*sp. nov.*	WiCl	1118
Section *Caulorrhizae*			
pintoi Krapov. & W. C. Gregory	*sp. nov.*	GK	12787
repens Handro	–	Otero	2999
Section *Erectoides*			
archeri Krapov. & W. C. Gregory	*sp. nov.*	KCr	34340
benthamii Handro	–	Handro	682
brevipetiolata Krapov. & W. C. Gregory	*sp. nov.*	GKP	10138
cryptopotamica Krapov. & W. C. Gregory	*sp. nov.*	KG	30026
douradiana Krapov. & W. C. Gregory	*sp. nov.*	GK	10556
gracilis Krapov. & W. C. Gregory	*sp. nov.*	GKP	9788
hatschbachii Krapov. & W. C. Gregory	*sp. nov.*	GKP	9848
hermannii Krapov. & W. C. Gregory	*sp. nov.*	GKP	9841
major Krapov. & W. C. Gregory	*sp. nov.*	Otero	423
martii Handro	*sp. nov.*	Otero	174
oteroi Krapov. & W. C. Gregory	*sp. nov.*	Otero	194
paraguariensis			
ssp. *paraguariensis* Chodat & Hassl.	–	Hassler	6358
ssp. *capibarensis* Krapov. & W. C. Gregory	*ssp. nov.*	HLKHe	565
stenophylla Krapov. & W. C. Gregory	*sp. nov.*	KHe	572
Section *Extranervosae*			
burchellii Krapov. & W. C. Gregory	*sp. nov.*	Irwin et al.	21163
lutescens Krapov. & Rigoni	–	Stephens	255
macedoi Krapov. & W. C. Gregory	*sp. nov.*	GKP	10127
marginata Gardner	–	Gardner	3103
pietrarellii Krapov. & W. C. Gregory	*sp. nov.*	GKP	9923
prostrata Benth.	–	Pohl	1836
retusa Krapov., W. C. Gregory & Valls	*sp. nov.*	VPtSv	12883
setinervosa Krapov. & W. C. Gregory	*sp. nov.*	Eiten & Eiten	9904
villosulicarpa Hoehne	–	Gehrt	SP47535

Table 6.2.   (*continued*)

Section and Species	Status	Collector[d]	Collection No.
Section *Heteranthae*			
dardani Krapov. & W. C. Gregory	*sp. nov.*	GK	12946
giacomettii Krapov., W. C. Gregory, Valls & C. E. Simpson	*sp. nov.*	VPzV1W	13202
pusilla Benth.	–	Blanchet	2669
sylvestris (A. Chev.) A. Chev.	–	Chevalier	486
Section *Procumbentes*			
appressipila Krapov. & W. C. Gregory	*s*p.nov.	GKP	9990
chiquitana Krapov., W. C. Gregory & C. E. Simpson	*sp. nov.*	KSSc	36027
kretschmeri Krapov. & W. C. Gregory	*sp. nov.*	KrRa	2273
lignosa[b] (Chodat and Hassl.) Krapov. & W. C. Gregory	*com. nov.*	Hassler	7476
matiensis Krapov., W. C. Gregory & C. E. Simpson	*sp. nov.*	KSSc	36014
rigonii Krapov. & W. C. Gregory	–	K	9459
subcoriacea Krapov. & W. C. Gregory	*sp. nov.*	KG	30037
vallsii Krapov. & W. C. Gregory	*sp. nov.*	VRGeSv	7635
Section *Rhizomatosae*			
Ser. *Prorhizomatosae*			
burkartii Handro	–	Archer	4439
Ser. *Rhizomatosae*			
glabrata			
var. *glabrata* Benth.	–	Riedel	1837
var. *hagenbeckii*[c] Benth. (Harms ex. Kuntze) F. J. Herm.	–	Hagenbeck	2255
pseudovillosa[c] (Chodat & Hassl.) Krapov. & W. C. Gregory	*com. nov.*	Hassler	5069
Section *Trierectoides*			
guaranitica Chodat & Hassl.	–	Hassler	4975
tuberosa Bong. ex Benth	–	Riedel	605
Section *Triseminatae*			
triseminata Krapov. & W. C. Gregory	*sp. nov.*	GK	12881

[a]See Table 1.

[b]Type Lectotype.

[c]Type Lecto holotype.

[d]Collectors: B = Banks, Cl = Claure, Cr =Cristobal, Fr = Fernandez, G = Gregory, Ge = Gerin, H = Hammons, He = Hemsy, K = Krapovickas, Kr = Kretchmere, L = Langford, Mr = Mroginski, P = Pietrarelli, Pt = Pittman, R = Rao, Ra = Raymon, S = Simpson, Sc = Schinini, St = Stalker, Sv = Silva, V = Valls, Ve = Veiga, Vl = Valente, W = Werneck, and Wi = Williams. Others = as listed.

aneuploid species ($2n = 2x = 18$). Diversity apparently occurred in the genus as species became separated into major drainage systems, and species of sections *Erectoides, Extranervosae,* and the diploids of section *Rhizomatosae* are believed to be most ancient. The center of genetic variation for the genus is the Mato Grosso region of Brazil to eastern Bolivia (Stalker et al. 1994). However, when specifically comparing *A. hypogaea* to other species, the greatest probability of finding unique genes is in the north-central, northeast, south, and southeast regions of Brazil. These are areas where species distantly related to the domesticated peanut are found and ones that are cross incompatible with *A. hypogaea.*

More than 1300 accessions of *Arachis* species have been collected (Stalker and Simpson 1995), and importantly, many of these are cross compatible with the domesticated species. *Arachis villosulicarpa,* which grows in the northeastern region of Mato Grosso, Brazil and *A. stenosperma,* which grows in central and southeast Brazil have also been grown for their seeds (Gregory et al. 1973; Simpson et al. 1993b). In the case of *A. stenosperma,* seeds were apparently carried either by the native people or missionaries from central Brazil to the southeast because plants of the species are found at abandoned missionary sites. Several species have been used for forages, including *A. glabrata* which has several cultivars under cultivation (Prine et al. 1986, 1990). Unfortunately, this species produces few seeds, and propagation is entirely through rhizomes. *Arachis pintoi* is cultivated as a forage in South America and Australia (Asakawa and Ramirez-R 1989; Cameron et al. 1989). This species produces large numbers of seeds and is relatively easy to establish under field conditions. Numerous other species have been used as ornamentals, including *A. repens* Handro, which is used extensively as a roadside and landscape plant in Central and South America (Stalker and Simpson 1995). Large plant breeding efforts have been undertaken since the mid-1950s to characterize species for agronomically useful traits (Lynch and Mack 1995; Stalker and Simpson 1995), and many accessions have been identified with high levels of disease and insect resistances.

III. REPRODUCTIVE DEVELOPMENT

The morphology, anatomy, and reproductive development of peanut has been described numerous times (Gregory et al. 1973; Rao 1988; Moss and Rao 1995) and will only be briefly described here. Inflorescences are borne in the axils of leaves on both primary and secondary branches.

They are simple or compound and each has up to five flowers. Only one flower per inflorescence usually opens on any given day. Flowers are papillionaceous and sessile, but appear to be stalked because of an elongated tubular hypanthium or calyx tube. Styles are contained within the calyx tube, and both the style and calyx tube rapidly elongate during the 12 to 24 h prior to anthesis and can reach a length of 5 cm or more. The hypanthium is attached to the base of the ovary, which is superior. The corolla consists of a standard, wing and keel petals, and the calyx has five sepals that are borne on the distal end of the elongated hypanthium. The standard ranges in color from deep orange to light yellow, and in rare cases it may be white. A central crescent area exists on the face of the standard that is usually darker in color, or in some cases a different color than the remainder of the standard (Moss and Rao 1995). Wings are usually the same color as the standard.

Flowers contain ten androecium, with five anthers being elongated and the remaining five being more globular and small. One or more anthers is usually sterile and difficult to observe. Maeda (1972) observed that sterility is more common in spanish and valencia types than in virginia types. Microsporogenesis in peanut was described by Xi (1991). Pollen is usually mature 6 to 8 h prior to anthesis (Pattee et al. 1991) and, at anthesis the pollen is two-celled and each cell has two nuclei. Stigmas are generally as long as or slightly shorter than the anthers. Both the stigma and anthers are enclosed by the keel, which induces self-fertilization. However, bees may be needed to trip flowers in some species, and these insects also carry pollen to other plants resulting in up to 8 percent outcrossing (Knauft et al. 1992). Pollination occurs at approximately the same time as anthesis, which occurs a few hours after sunrise (Pattee et al. 1991). The stigmatic surface contains enzymes that promote pollen adhesion (Lu et al. 1990), and within 8 h after anthesis these enzymes apparently degrade. Thus, the most successful crossing in artificial hybridization programs occurs during the early morning hours. In contrast to the large stigmatic surface of *A. hypogaea* and other annual species in the genus, perennials have small stigmas which are surrounded by hairs, that greatly limit the number of pollen grains that can adhere to the receptive surface (Lu et al. 1990). This may account for annuals being much better seed parents than perennials in crossing programs, as well as generally producing greater numbers of seeds in germplasm nurseries.

The ovary of peanut is unilocular and usually has one to three ovules. The embryo sac has a prominent egg, and starch grains surround the endosperm nucleus. After fertilization, the starch grains disappear, and a multicellular proembryo develops (Pattee and Stalker 1991). The

flower petals then wither within 24 hours, but the hypanthium and style usually remain attached to the base of the ovary for up to five days (Pattee and Mohapatra 1986). The proembryo divides three to four times (resulting in an 8 to 16 nucleate egg) and then becomes quiescent at the time when a meristem located adjacent to the basal ovule becomes active. A carpophore (or gynophore, but commonly called a "peg") begins to elongate with positive geotropism into the soil (Zamski and Ziv 1976). After the peg enters the soil it becomes diageotropic (i.e., begins to grow horizontally), ceases to elongate, and at the same time it swells, and the embryos resume cell division. Pods usually develop in the absence of light (Ziv 1981), but aerial pods can occur. In *A. hypogaea,* pod development generally begins 16 to 17 days after pollination, but in other species the process may be delayed until 23 to 25 days (Halward and Stalker 1987a). Pegs of the domesticated species are relatively short and do not break easily, but pegs of *Arachis* species may be a meter or more in length and are fragile.

The seed has two cotyledons, a hypocotyl, epicotyl, and radicle. The cotyledons comprise nearly 96 percent of the seed weight and are the major storage tissue for the developing seedlings (Moss and Rao 1995). The seeds contain about 20 percent carbohydrates, 45 percent oil (Ahmed and Young 1982), and 25 percent protein (Amaya et al. 1977); but a considerable range in oil and protein percentage exists among genotypes. Most peanuts are deficient in lysine and tryptophane, and allergens are associated with seed storage proteins (Burks et al. 1998).

IV. CYTOGENETICS AND GENOMES

Both diploid ($2n = 2x = 20$) and tetraploid ($2n = 4x = 40$) species have evolved in the genus, and three species have been identified with 18 chromosomes, including *A. decora* Krapov., W. C. Gregory and Valls, *A. palustris* Krapov., W. C. Gregory and Valls, and *A. praecox* Krapov., W. C. Gregory and Valls (Lavia 1996, 1998; Krapovickas and Lavia 2000). This is surprising since trisomics are rather common in shriveled seeds of *A. hypogaea,* but monosomics are extremely rare (Stalker 1985b). Tetraploids are found in section *Arachis,* including *A. hypogaea* and *A. monticola* Krapov. and Rigoni, and in sections *Extranervosae* and *Rhizomatosae.* Polyploidy is believed to have originated independently in different sections (Smartt and Stalker 1982), and diploids are likely to be more ancient than tetraploids. The chromosomes of *Arachis* species are small, ranging from 1.4 to 3.9 µm in length, and several species have been karyotyped (Stalker and Dalmacio 1981; Singh and Moss 1982;

Stalker 1985a, 1991; Lavia 1998). Species in section *Arachis* generally have metacentric chromosomes, with the exception of *A. glandulifera* Stalker, which is highly asymmetrical (Stalker 1991). Six chromosomes appear to have little karyotypic change, whereas the nucleolus organizer region is found in different positions on the seventh chromosome, and there have been many structural changes in the other three chromosomes of *Arachis* species (Murty et al. 1985; Bharathi et al. 1983; Kirti et al. 1983; Jahnavi and Murty 1985). Based on their observations, species in sections *Erectoides, Extranervosae,* and *Triseminatae* are more ancient than species in sections *Arachis* and *Rhizomatosae.*

Section *Arachis* is important because the domesticated peanut belongs in the group and introgression from closely related species should be easier than from more distantly related species. Three genomes have been defined in section *Arachis,* including the A genome found in most species; the B genome species as represented by *A. batizocoi* Krapov. and W. C. Gregory, *A. ipaensis* Krapov. and W. C. Gregory, *A. cruziana* Krapov., W. C. Gregory and C. E. Simpson (Burow et al. 1997b), and likely *A. williamsii* Krapov. and W. C. Gregory (Lavia 1996; Tallury et al. 2001), *A. hoehnei* Krapov. and W. C. Gregory, and *A. magna* Krapov., W. C. Gregory & C. E. Simpson (S. P. Tallury, pers. comm. 2001); and the D genome is represented by *A. glandulifera* (Stalker 1991). Translocations appear to be common in *A. batizocoi* (Stalker et al. 1991a), and the nucleolar organizer chromosome is karyotypically different in botanical varieties of *A. hypogaea* (Stalker and Dalmacio 1986). Other genomes have been proposed in sections *Ambinervosae* (Am) [*Ambinervosae* was changed to *Heteranthae* by (Krapovickas and Gregory 1994)], *Erectoides* (E), *Caulorhizae* (C), *Extranervosae* (Ex), and *Triseminalae* (T) (Smartt and Stalker 1982). Tetraploids in section *Rhizomatosae* appear to have similarities to the genomes of sections *Erectoides* and *Arachis* (Stalker 1981b, 1985a).

Arachis hypogaea is believed to be an allotetraploid species, in large part because of karyotypic differences in chromosomes where only one distinctively small chromosome pair is observed and the diploid-like chromosome pairing during meiosis. Smartt and Gregory (1967) concluded that *A. hypogaea* has A and B genomes. Kochert et al. (1991) supported this conclusion because RFLP analyses showed that most gel lanes had two bands in *A. hypogaea* and only one band in diploids. Molecular data indicates that the domesticated peanut had a single-event origin and that introgression from related species has been extremely limited (Kochert et al. 1996). Only one additional tetraploid species belongs to section *Arachis* (*A. monticola*) which Stalker and Simpson

(1995) concluded is a weedy derivative of *A. hypogaea* rather than its progenitor.

Hybridization of species between different sections of *Arachis* is possible, but the F_1s are completely sterile (Gregory and Gregory 1979). Using amphiploids of species in closely related sections to produce hybrids can enhance cross compatibility, and chromosome homologies can be detected; but Stalker (1981a) reported that progenies of section *Erectoides × Arachis* hybrids were sterile and fertility restoration was impossible. Hybridization of species within a section produce results ranging from progenies with complete sterility to ones having a high level of fertility. In section *Arachis,* hybrids between A-genome species produce progenies with relatively high fertility levels and 10 bivalents (Stalker and Moss 1987; Stalker et al. 1991b). Hybrids between A-genome and either B- or D-genome species have four to eight univalents and plants are sterile (Stalker et al. 1991b).

V. GENETIC RESOURCES

A. Collections

The domesticated peanut was carried by the Spaniards to Malaysia, China, Indonesia, and Madagascar (Krapovickas 1969). The peanut also moved eastward to Europe and then to Africa. Peanuts were likely introduced into North America from Brazil by way of slave ships that were resupplied in northeastern Brazil to complete the voyage (Stalker and Simpson 1995).

The most common method of collecting peanut has been to gather samples in small markets in the primary and secondary centers of diversity in South America. A large amount of diversity exists in these markets because local farmers grow an array of genotypes. Samples are typically separated based on pod and seed characteristics (Stalker and Simpson 1995). Many markets have yielded up to 30 accessions, and Stalker and Simpson (1995) noted one market in Brazil that yielded 86 distinct lines. A greater amount of agronomic data can be obtained when collections are directly made from farmer's fields. However, travel to individual locations is very time-consuming and in many cases, travel to remote areas is difficult because of poor or nonexisting roads. Limited seed supply that is being saved for the next growing season is also problematic because farmers must retain ample seed stocks for planting during the following year. Sampling strategies for peanut have been summarized by Simpson (1985), who concluded that a 1 kg sample of

seed is sufficient when the seeds are visually homogeneous for adequate division between the donor country and the participants on a collection trip, but larger samples are needed if variation exists. Because of the large seed size of peanut, handling large samples on germplasm expeditions is difficult. From 1959 to date, there have been more than 40 collection trips in South America for *A. hypogaea* and related peanut species (Stalker and Simpson 1995). In addition, J. Smartt introduced a large number of *A. hypogaea* accessions into the United States from Africa during the 1960s and a large number of accessions were also introduced from Israel in the 1970s by Dr. A. Ashri.

The USDA germplasm collection numbers over 8000 accessions of *A. hypogaea* (Holbrook 2001) and about 800 accessions of *Arachis* species (Stalker and Simpson 1995). Large *Arachis* species collections are also maintained at Texas A&M, N. C. State University, the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) in India, and at the National Center of Genetic Resources (CENARGEN) in Brazil. The largest collection of domesticated peanut is at ICRISAT, where there are 14,310 accessions from 92 countries and 413 accessions of *Arachis* species (Upadhyaya et al. 2001a). Descriptor lists have been published for *A. hypogaea* by International Board for Plant Genetic Resources (IBPGR) and ICRISAT (1992) and the USDA (Pittman 1995). Simpson et al. (1992) applied 53 of the descriptors to 2000 lines and observed a large amount of variation in pod and seed characters. Although the plant descriptions outline the basic structure of variation in *A. hypogaea,* many intermediates exist, and the taxonomy of the cultivated peanut is not always clear. A large number of accessions in the ICRISAT collection have been evaluated for morphological traits, water use efficiency, and reactions to many disease and insect pests of peanut (Upadhyaya et al. 2001a). Accessions in the U.S. collection have not been evaluated as extensively as the ones at ICRISAT.

Williams (2001) discussed using the geographic information system (GIS) to more effectively study, locate, and conserve *Arachis* genetic resources. Based on existing germplasm collections and geographical distribution of genetic diversity, Williams (2001) concluded that additional collection of wild *Arachis* species is warranted in eastern Bolivia and northwestern Paraguay. Several areas within primary and secondary centers of diversity that warrant further collection of the cultivated species were also listed.

Preservation of accessions in the *A. hypogaea* collection is generally straightforward and regeneration decisions are based on the total number and age of seeds available in storage, and the number of requests made by the user community. Both the USDA peanut curator and plant breed-

ers from private industry, state-funded universities, and the USDA have taken a vested interest in the germplasm collection and have cooperated to assure adequate seed reproduction. Sanders et al. (1982) indicated that the sum of temperature (F) plus relative humidity should be less than 100 to have optimal seed storage. Under ideal storage conditions, peanuts remain viable for 15 or more years, and A. J. Norden (pers. comm. 1990) stored seeds for 20 years with good germination percentages when seeds were stored at 10°C and 45 percent relative humidity.

Wild *Arachis* accessions are more difficult to maintain than ones of the domesticated peanut. Species of *Arachis* occupy a wide range of habitats in South America, and accessions can be lost before adequate growing conditions under cultivation can be discovered, especially for species that produce few seeds. Both annual and perennial species exist in nature, and the annuals generally produce greater numbers of seeds than perennials. Of the more than 1300 *Arachis* wild species accessions that have been collected, about 800 remain in germplasm nurseries (Stalker and Simpson 1995). *Arachis marginata* Gardner is an example of a species that is very difficult to maintain in the United States because its plants grow very slowly and are weak. The *Triseminales* species *A. tuberosa* Benth. and *A. guaranitica* Chodat and Hass1. enter permanent dormancy when seeds are dried, but seeds have been kept viable for several years in moist sphagnum moss. Under long day conditions, many species flower profusely but do not produce pegs; whereas under short day conditions, many species have a very high reproductive efficiency but do not produce many flowers (Stalker and Wynne 1983). At the autumnal and vernal equinoxes, many species produce sufficient numbers of flowers and pegs to greatly increase seed numbers of plants derived from either self-pollination or interspecific hybrids (Stalker unpublished data). More than 25 percent of the species accessions currently in germplasm nurseries (especially the *Rhizomatosae* species) produce very few seeds and are maintained as vegetative materials in greenhouses. Many perennial species will not produce seeds when grown under greenhouse conditions and only a few seeds when propagated in the field. Stalker and Simpson (1995) indicated that 23 percent of the *Arachis* collection have fewer than 50 seeds in storage at any of the sites where peanuts are maintained.

Because peanuts produce pegs, either placing pots close to each other in the greenhouse or failing to isolate plots in the field can result in seed mixtures. Several curators only propagate the wild species collection under greenhouse conditions, but this results in few seeds being produced and restricts evaluations for agronomically useful traits. At North Carolina State University, plots are grown in blocks that are 5 to 10 m

apart in all directions, and accessions of cross-incompatible species are grown adjacent to each other. This greatly reduces outcrossing, but very low levels of cross-contamination have been found between plots containing the same species even when they were separated by incompatible accessions. Species of sections *Arachis, Erectoides,* and *Procumbentes* appear to outcross more than species in other sections of the genus.

B. Germplasm Exchange

Germplasm exchange has become more difficult during recent years as countries have imposed more strict quarantine policies. Diseases such as rosette virus are found only in Africa, and other production areas have attempted to avoid introducing this virus. A one- to two-year observation period under greenhouse conditions is generally imposed to restrict introductions of unwanted diseases. The USDA Plant Introduction Station at Griffin, Georgia has routinely screened introductions for peanut stripe *Potyvirus* (PStV) using bioassays since the mid-1980s. Property right issues have not greatly affected the movement of peanut germplasm within the United States, but since the Convention on Biological Diversity in 1993, international seed exchange has become significantly more tedious and restricted (Williams and Williams 2001). Germplasm obtained prior to 1993 at the CGIAR Centers, including ICRISAT which has a mandate to preserve *Arachis* genetic resources, is freely available; but germplasm obtained since then is subject to the terms of the Convention on Biological Diversity. Fortunately, a memorandum of understanding has been signed by the USDA and ICRISAT to facilitate exchange of germplasm (Shands and Bertram 2000). Both institutions have agreed to forego claims of ownership and intellectual property rights on exchanged germplasm. The same policy applies to germplasm forwarded to state or private institutions when it is passed through the USDA (Williams and Williams 2001).

In addition to restricting exchange of germplasm already in collections, field collections have also been hindered since implementation of the Convention on Biological Diversity. Leaders of many countries wish to have monetary compensation for germplasm and they do not recognize advantages of in-kind benefits, such as storage and maintenance, sharing herbarium and seed collections, joint publication, and research (Williams and Williams 2001). Williams and Williams (2001) reported making special arrangements with the governments of Ecuador and Paraguay so they could collect peanut in these countries. Host scientists were actively involved in collection trips, and the benefits to those countries were

clearly established prior to collecting seeds. For example, in Ecuador, rather than immediately sending seeds to the United States after collecting samples, they planned a seed-increase nursery in the host country. They also arranged for the materials to be characterized in Ecuador under contract to the USDA and both countries then had access to the data set prior to the germplasm being exported. For a collection expedition in Paraguay, the USDA agreed to store germplasm at the United States National Seed Storage Lab because there are no genebank facilities in that country. Their efforts should serve as a model for collection of peanut and other crop species in these and other countries.

C. Core Collections

The U.S. *A. hypogaea* collection contains a great amount of genetic diversity, but the germplasm has not been extensively used in cultivar development (Knauft and Gorbet 1989). Ironically, the size of the collection has limited its use because of the costs associated with screening all accessions for traits that could be used in cultivar development.

A core collection (Frankel 1984; Frankel and Brown 1984) was developed for the U.S. *A. hypogaea* germplasm collection by Holbrook et al. (1993). Data on peanut in the Germplasm Resource Information Network (GRIN) <http://www.ars-grin.gov> were used for selecting entries, and included country of origin and measurements on plant type, pod type, seed size, testa color, number of seeds per pod, and average seed weight. Available information on accessions varied from only the country of origin to information for all seven variables. The U.S. germplasm collection was first stratified by country of origin and then divided into nine sets based on the amount of additional information available for accessions and on the number of accessions per country of origin. This procedure resulted in the selection of 831 accessions from the U.S. *A. hypogaea* germplasm collection. Accessions included in the core collection are noted in GRIN. To maximize the usefulness of the peanut core collection, the relationship between the individual accessions and the clustering procedure used in its development is available to users (holbrook@tifton.cpes.peachnet.edu). The first format lists accessions in numerical order so that the cluster designation for individual accessions can be rapidly determined. The second file lists accessions by clusters so that all accessions within a cluster can be rapidly determined.

The core collection approach to germplasm evaluation is a two-stage approach. The first stage involves examining all accessions in the core collection for a desired characteristic. This information is then used to

determine which clusters of accessions in the entire germplasm collec-
tion should be examined during the second stage of screening. Theo-
retically, the probability of finding additional accessions with a desired
characteristic would be highest in these clusters.

Holbrook and Anderson (1995) used data on resistance to late leaf spot
[*Cercosporidium personatum* (Berk. & M. A. Curtis)] that was available
for the entire peanut germplasm collection to retrospectively determine
how effective the use of this core collection would have been for iden-
tifying sources of resistance in the entire collection. Disease ratings for
the core accession(s) representing each cluster were defined as the indi-
cator value for that cluster. Data were first examined to determine how
many leaf spot resistant accessions would have been identified by exam-
ining the core collection. Data were also examined to determine how many
leaf spot resistant accessions would have been identified by examining
all accessions from clusters having a resistant indicator value. The use
of a two-stage screening approach on this peanut core collection would
have resulted in the identification of 61 leaf spot resistant accessions.
This approach would have required screening 27 percent of the entire
collection and would have identified 54 percent of the resistant acces-
sions in the entire collection. In addition, the best four (and eight of the
best ten) sources of resistance in the entire collection would have been
identified.

Holbrook et al. (2000c) also evaluated the effectiveness of a two-stage
core screening approach in identifying resistance to the peanut root-knot
nematode [*Meloidogyne arenaria* (Neal) Chitwood race 1] in the U.S.
germplasm collection of peanut. Accessions from 30 clusters having
resistant indicator values and from four clusters having susceptible in-
dicator values were tested for resistance in greenhouse trials. The effi-
ciency of identifying resistance to the peanut root-knot nematode in
clusters having resistant indicator values was significantly better than
the success rate in clusters having susceptible indicator values. These
results demonstrated that the use of a two-stage screening approach
with a core collection could improve the efficiency of identifying valu-
able genes in germplasm collections.

A major benefit of having a peanut core collection has been a signifi-
cant increase in peanut germplasm evaluation work (Holbrook 1999). In
the United States, peanut is a regional crop with relatively few individ-
uals involved in breeding and genetic research. The development of a
peanut core collection has allowed germplasm evaluations that require
fewer resources. Anderson et al. (1996a) screened the peanut core col-
lection for resistance to tomato spotted wilt virus (TSWV), which is
among the greatest yield-reducing viruses affecting peanut. The peanut

core collection provided a logical subset of peanut germplasm that could be rapidly screened and they identified 55 accessions with resistance.

Isleib et al. (1995a) screened the peanut core collection for resistance to cylindrocladium black rot (CBR) initiated by *Cylindrocladium parasiticum* Crous, Wingefield, et Alfenas and to early leaf spot (*Cercospora arachidicola* Hori). In a greenhouse screening trial, 11 core accessions had greater resistance to CBR than NC 3033, the resistant check. In field trials, 12 early maturing core accessions had a level of resistance to early leaf spot similar to that of GP-NC 343, the resistant check. Twelve medium or late maturing lines had less defoliation than the resistant check.

Because of the high costs associated with evaluating peanut for preharvest aflatoxin contamination (PAC), it is not feasible to examine the entire collection for resistance to PAC. Use of the peanut core collection has resulted in the first report of field resistance to PAC in the U.S. peanut germplasm collection (Holbrook et al. 1998c). Fourteen accessions averaged 70 percent reduction in PAC and six of these accessions exhibited a 90 percent reduction in PAC in multiple years of testing. The development of the peanut core collection was essential for conducting this research.

The most agronomically acceptable portion of the core collection also has been evaluated for resistance to Rhizoctonia limb rot (*Rhizoctonia solani* Kuhn, AG-4) (Franke et al. 1999). This subset of the core collection consisted of 66 accessions having a spreading or spreading-bunch growth habit. Six core accessions had a high level of resistance to Rhizoctonia limb rot.

The peanut core collection has provided a logical subset of the entire germplasm collection that can be extensively examined for traits other than disease resistance. Holbrook and Anderson (1993) measured plant descriptor information for all accessions in the core collection. Using data from eight above ground and nine below ground descriptors, Holbrook (1997) concluded that additional peanut accessions should be collected from Columbia, Venezuela, Uruguay, and possibly Bolivia to increase variation in the entire collection. Accessions in the core collection also have been used to identify genetic variation for oil content (Holbrook et al. 1998a) and fatty acid composition (Hammond et al. 1997).

A second core collection has been developed to represent the *A. hypogaea* germplasm maintained by ICRISAT (Upadhyaya et al. 2001b). This core collection was developed from a total of 14,310 accessions using an approach slightly different from that used by Holbrook et al. (1993). The ICRISAT peanut collection was first stratified by botanical variety within subspecies, and then stratified by country of origin.

Accessions of the same botanical variety but from small and adjacent countries with similar agro-climates were grouped together. This resulted in 75 groups, and accessions within each group were then clustered using multivariate statistical analysis. Approximately 10 percent of the accessions from each cluster were randomly sampled resulting in a core collection consisting of 1704 entries.

VI. BREEDING PEANUT

A. Conventional Breeding Methods

Standard breeding methods for self-pollinated crops have been used to develop peanut cultivars and several reviews have been published (Isleib and Wynne 1992; Isleib et al. 1994; Knauft and Ozias-Akins 1995; Knauft and Wynne 1995). Although mutation breeding methodologies were used extensively in the late 1950s to early 1970s, the materials produced in the United States were not widely utilized by producers. Thus, mutation breeding is little used by the present-day peanut breeding community. Mass selection also is used infrequently in peanut because of negative correlations between disease resistance and yield (Knauft and Wynne 1995). Pedigree breeding is commonly used in peanut, and back-cross methodologies are becoming more frequent as useful qualitatively inherited traits are identified. Use of single seed descent methods has greatly increased in recent years. Isleib et al. (1994) indicated that there are advantages to this method to save space and resources. Recurrent selection has received little attention in peanut breeding because of efforts needed to make a large number of crosses, but Halward et al. (1991) concluded that selection progress for multiple traits could be made in an *A. hypogaea* × *A. cardenasii* Krapov. & W. C. Gregory interspecific hybrid. Production of F_1 hybrids is not a viable option in peanut because of the difficulties encountered in making a large number of crosses. There does not appear to be a large advantage to early generation testing in peanut, in large part because most breeding efforts with the crop are for quantitatively inherited traits.

Genotype × environment interactions are widespread in peanut, and multi-year and multi-location testing is necessary prior to cultivar release. These interactions were reviewed by Knauft and Wynne (1995), so the following discussion will focus on research activity since their review. Since 1995, there have been many investigations related to breeding peanut with resistance to the peanut root-knot nematode, TSWV, PAC, and fungal pathogens. Research has also been published

related to improving roasted peanut flavor and oil quality and drought tolerance.

Some of the aforementioned traits are conditioned by one or two major genes, and many peanut breeding programs are using backcrossing methods to incorporate these traits into cultivars. Isleib (1999) examined the factors affecting the probability of recovering progeny homozygous for more desirable alleles than either parent. Probabilities for various combinations of these factors were presented and can be used by plant breeders to assist in choosing selection procedures that will maximize the chance of recovering desirable plants from biparental populations. Isleib (1997) compared the cost-effectiveness of different breeding procedures when the relative costs of crossing, selfing, and evaluation of progeny are known.

Reducing input costs associated with pest management is becoming increasingly important in the United States due to changes in the federal peanut program that have significantly reduced commodity support prices (Jordan et al. 1999). Growing peanut cultivars with disease resistance will cut costs of production and allow United States production to become more competitive with world market prices. Although several programs during the 1980s had been initiated to breed for resistance to diseases, few disease-resistant cultivars had been released before 1990 because of the short duration of these efforts (Wynne et al. 1991b). However, many sources of disease resistance were identified in the germplasm collection and incorporated into peanut breeding programs. The use of this germplasm is just beginning to have significant economic impacts on United States peanut farmers. Isleib et al. (2001) summarized the use of genetic resources in peanut cultivar development and estimated that resistant cultivars have had an economic impact of more than $200 million annually for U.S. peanut producers. The largest positive impact on peanut production has come through development of cultivars with resistance to Sclerotinia blight, root-knot nematode, and TSWV.

1. Resistance to Nematodes. The peanut root-knot nematode causes significant economic losses in many peanut production areas of the world. Chemicals for control of this pest are becoming increasingly limited, and the development of peanut cultivars with resistance is desirable. Holbrook and Noe (1992) evaluated 1321 *A. hypogaea* plant introductions for resistance to *M. arenaria* and identified 17 accessions that supported fewer egg masses and seven genotypes that supported less egg production per gram of fresh root weight compared with the susceptible cultivar, 'Florunner'. Holbrook et al. (1996) evaluated an additional 1000

plant introductions and identified eight accessions that had significantly fewer egg masses than 'Florunner'. Although none of the eight had significantly higher levels of resistance than those reported by Holbrook and Noe (1992), two exhibited significantly higher yields than other entries when grown in soil heavily infested with *M. arenaria*.

Holbrook et al. (2000b) tested 741 accessions from the U.S. peanut core collection for resistance to *M. arenaria*. Thirty-six core accessions showed a reduction in root galling, egg-mass ratings, egg count per root system, and egg count per gram of root in comparison to the susceptible check, 'Florunner'. Holbrook et al. (2000c) evaluated accessions from 30 clusters having resistant indicator accessions. This second stage screening identified 259 accessions that had reduced egg-mass production and 28 that had greatly reduced numbers of egg masses. Relatively large numbers of resistant accessions were from China and Japan compared with the percentage of the germplasm collection that originated from these countries.

Researchers have identified many sources of resistance in the U.S. germplasm collection from various geographical origins. Resistant peanut breeding lines that produce greater yield than susceptible cultivars when grown in soil heavily infested with *M. arenaria* have also been identified (Holbrook et al. 1998b). However, only moderate levels of resistance have been observed originating from *A. hypogaea*. Timper et al. (2000) examined the expression of different mechanisms of resistance in six moderately resistant genotypes from various geographical locations. If different mechanisms were involved, then it should be possible to combine the mechanisms to improve the level and durability of the resistance. The primary expression of resistance in these six genotypes was similar and appears to be a reduction in the percentage of second-stage juveniles (J2) that establish a functional feeding site.

Very high levels of resistance to *M. arenaria* exist in *Arachis* species (Baltensperger et al. 1986; Nelson et al. 1989; Holbrook and Noe 1990), and resistance has been introgressed into *A. hypogaea*. Stalker et al. (1995b) introgressed nematode resistance into *A. hypogaea* ($2n = 4x = 40$) from *A. cardenasii* ($2n = 2x = 20$). Garcia et al. (1996) reported that this resistance was conditioned by two dominant genes where one gene (*Mag*) inhibited root galling and another gene (*Mae*) inhibited egg production by *M. arenaria*. Resistance to *M. arenaria* also has been introgressed into *A. hypogaea* by using a complex interspecific hybrid [released as TxAG-6 by Simpson et al. (1993a)] from the three nematode resistant species, *A. batizocoi, A. cardenasii,* and *A. diogoi* Hoehne (Simpson 1991). TxAG-7 was derived from the first backcross generation of *A. hypogaea* cv. 'Florunner' × TxAG-6 (Simpson et al. 1993a).

Resistance to *M. arenaria* in *A. cardenasii* was reported to completely inhibit nematode development and was accompanied by an apparent necrotic, hypersensitive host reaction (Nelson et al. 1990). The resistance of *A. batizocoi* caused a reduction in the total number of invading nematodes that reached maturity and produced eggs, and increased the time required for *M. arenaria* to complete its life cycle. No hypersensitive reaction was observed in *A. batizocoi* (Nelson et al. 1990). The resistance of TxAG-7 was similar to that of *A. cardenasii,* except that no host-cell necrosis characteristic of a hypersensitive reaction was associated with invading J2s (Starr et al. 1990). In addition to resistance to *M. arenaria,* TxAG-6 and TxAG-7 also have resistance to *M. javanica* and an undescribed *Meloidogyne* sp. (Abdel-Momen et al. 1998). A back-crossing program was used to introgress the root-knot nematode resistance from TxAG-7 into peanut breeding populations (Starr et al. 1995). This work resulted in the release of 'COAN', the first peanut cultivar with resistance to *M. arenaria* (Simpson and Starr 2001). This resistance is conditioned by a single dominant gene. The yield potential of 'COAN' is slightly less than that of its recurrent parent, 'Florunner' (Starr et al. 1998), but Church et al. (2000) observed significantly higher yield potential in nematode resistant breeding lines that resulted from two additional backcross generations. However, 'COAN' is extremely susceptible to TSWV (Holbrook et al. 2000d).

Breeding for nematode resistance represents the first practical use of marker-assisted selection (MAS) in peanut. Burow et al. (1996) identified three RAPD markers (RKN 229, RKN 410, and RKN 440) linked to *M. arenaria* resistance in several breeding populations derived from TxAG-7 in the fifth backcross generation. The resistance in each of the populations appeared to have been derived from *A. cardenasii* and was most likely due to a single gene. Subsequent studies (Choi et al. 1999) confirmed that the resistance in some of these populations was conferred by a single dominant gene from *A. cardenasii.* However, data from other populations indicated the possibility of a second gene for resistance. Choi et al. (1999) also evaluated the utility of three RFLP probes for use in selecting individuals homozygous for resistance in a segregating population. Resistant and susceptible alleles for RFLP loci R2430E and R2545E were relatively easy to score and both were sufficiently close to the resistance allele to be used with a high degree of confidence. The third loci, S1137E is more distant from the resistant gene and is less reliable as a selectable marker.

2. Resistance to Soilborne Diseases. The most important soilborne diseases of peanut in the United States are white mold (*Sclerotium rolfsii*

Sacc.), Sclerotinia blight (*Sclerotinia minor* Jagger), and Cylindrocladium black rot (CBR) (*C. parasiticum*). White mold is found throughout the major peanut growing areas of the United States and causes the greatest yield losses of all diseases (Backman and Brenneman 1997). Genetic variation for resistance to white mold exists in *A. hypogaea,* and sources of resistance have been identified (Branch and Csinos 1987; Smith et al. 1989; Grichar and Smith 1992).

Shokes et al. (1996) found that field screening was more consistent than greenhouse tests for evaluating genotype responses to white mold. The nonuniform spatial distribution of natural inoculum can be a problem for field evaluations (Shew et al. 1984) and sterilized oat seed inoculated with *S. rolfsii* has been used to increase pathogen populations and improve the uniformity of fungal distribution (Shew et al. 1987; Brenneman et al. 1990; Shokes et al. 1996). However, even with uniform inoculum distribution, individual plants may escape the disease. Shokes et al. (1996) developed an inoculation method, termed the 'agar disk technique', which can be used to inoculate individual plants to prevent escapes. This technique has been used to identify resistant breeding lines (Shokes et al. 1998).

Several cultivars with moderate resistance to white mold are available to producers. 'Southern Runner' (Gorbet et al. 1987), initially released as a cultivar with partial resistance to late leaf spot, was also found to have moderate resistance to white mold (Brenneman et al. 1990; Grichar and Smith 1992; Branch and Brenneman 1993). Gorbet et al. (1997) also observed some resistance to white mold in 'Toalson' (Simpson et al. 1979), 'Pronto' (Banks and Kirby 1983), 'Georgia Browne' (Branch 1994), and 'Sunbelt Runner' (Mixon 1982). 'Tamrun 96' (Smith et al. 1998) has shown superior resistance to white mold when compared to other commonly grown cultivars (Besler et al. 1997, 2001).

Genetic variation for resistance to CBR has been observed in *A. hypogaea* and in general, spanish cultivars are most resistant, valencia cultivars are the most susceptible, and virginia cultivars are moderately susceptible (Phipps and Beute 1997). However, CBR-resistant lines of each type have been described and the partially resistant virginia-type cultivars, 'NC 8C' (Wynne and Beute 1983), 'NC 10C' (Wynne et al. 1991a), and 'NC 12C' (Isleib et al. 1997) have been released. The earlier cultivars had seed characteristics that were only marginally acceptable to manufacturers, and the newer release has more acceptable seed traits and higher yields. The inheritance of resistance is complex (Green et al. 1983), and the resistance appears to delay the onset of epidemics rather than the rate of disease progress (Culbreath et al. 1991). Recently,

Kucharek et al. (2000) observed partial resistance to CBR in cultivars and a breeding line that also has resistance to tomato spotted wilt virus.

Sclerotinia blight is the most important soilborne disease of peanut in Virginia and Oklahoma (Porter and Melouk 1997). Sources of resistance to *S. minor* have been identified (Coffelt and Porter 1982; Melouk et al. 1989; Akem et al. 1992; Porter et al. 1992), and several moderately resistant cultivars and germplasm lines have been released (Coffelt et al. 1982, 1994; Smith et al. 1990, 1991; Kirby et al. 1998). Peanut cultivars with spanish ancestry appear to be more resistant to Sclerotinia blight than cultivars or breeding lines from valencia or virginia backgrounds (Akem et al. 1992). Wildman et al. (1992) reported that at least two loci are involved in the inheritance of resistance. Screening techniques for identifying resistance have been developed (Brenneman et al. 1988; Melouk et al. 1992) that rely on rate of lesion growth and development. The age and/or developmental stage of the lateral limbs of plants have a marked effect on lesion development (Brenneman et al. 1988), and the younger and more succulent tissues are more susceptible to the disease. Melouk et al. (1992) developed a detached shoot technique that can be used to assess resistance to Sclerotinia blight in peanut genotypes. Goldman et al. (1995) reported that significant progress had been made in developing runner-type peanut breeding lines with resistance to Sclerotinia blight using field and greenhouse screening tools. Lines derived from interspecific crosses between *A. hypogaea* and *A. cardenasii* appear to be highly resistant in field experiments (J. Bailey, pers. comm. 2001), and the material should lead to highly resistant cultivars.

3. Resistance to Foliar Diseases. Early leaf spot (*C. arachidicola*) and late leaf spot (*C. personatum*) are the most damaging diseases of peanut worldwide (Shokes and Culbreath 1997). Sources of resistance to both early and late leaf spot have been identified in *A. hypogaea* (Chiteka et al. 1988a,b; Anderson et al. 1993), and used to develop breeding lines with resistance (Gorbet et al. 1982; Melouk et al. 1984; Wells et al. 1994; Xue and Holbrook 1998, 1999a,b; Branch and Fletcher 2001). Holbrook and Isleib (2001) observed that resistance to late leaf spot was more frequent than expected in *A. hypogaea* accessions which originated in Bolivia, and this country was also a valuable source of origin for resistance to early leaf spot. Although just one leaf spot pathogen usually predominates in a production region, both leaf spot species are generally found in a single field. Shifts in leaf spot species also have been observed over a period of years in the Virginia–Carolina production region. Although commonly used fungicides control both *C. arachidicola* and

C. personatum, cultivars with resistance to both pathogens will be needed to completely suppress the two leaf spot diseases.

Inheritance of resistance to leaf spots is complex (Kornegay et al. 1980; Anderson et al. 1986, 1991; Green and Wynne 1987; Iroume and Knauft 1987a,b; Jogloy et al. 1987), and several components contribute to resistance, including initial infection, lesion size, sporulation, and defoliation (Green and Wynne 1986; Chiteka et al. 1988a,b; Anderson et al. 1993; Waliyar et al. 1993, 1995). Resistance to leaf spot in peanut has generally been associated with late maturity (Norden et al. 1982; Miller et al. 1990). However, Branch and Culbreath (1995) documented a breeding line that had early maturity and tolerance to leaf spot. Aquino et al. (1995) found that latent period and maximum percentage of lesions that sporulated were the components of resistance most highly correlated with late leaf spot disease development. They suggested that using either of these two components to evaluate breeding populations may facilitate more rapid selection of lines with improved levels of rate-reducing resistance.

Until the release of 'Southern Runner' in 1984, no commercial cultivars were available with meaningful resistance to late leaf spot. The level of resistance in 'Southern Runner' is moderate, and fungicide applications are still needed to obtain optimum yields. Moderate levels of resistance are also available in the cultivars 'Florida MDR 98' and 'C-99R' (Gorbet et al. 1999).

Very high levels of resistance or immunity to the leaf spot diseases occur in related wild species of peanut (Stalker and Moss 1987; Stalker and Simpson 1995). Programs are ongoing to introgress this resistance into *A. hypogaea* (Stalker and Beute 1993). Ouedraogo et al. (1994) reported that resistance to both *C. arachidicola* and *C. personatum* was introgressed from wild species into productive runner-type breeding lines. Although the resistance was equal to or better than that of 'Southern Runner', it was less than the level of resistance observed in the wild species. Stalker and Mozingo (2001) reported associations of RAPD markers with resistance to *C. arachidicola* in an interspecific hybrid with *A. cardenasii* in the pedigree. Breeding progress has been made to suppress both early and late leaf spots, but combining high levels of resistance into high-yielding cultivars with acceptable market traits continues to be very difficult.

4. Resistance to Tomato Spotted Wilt Virus. Since 1985, TSWV has become a major disease problem in the peanut producing areas of the United States. The disease is now common in most peanut-growing areas, including Georgia, Florida, Alabama, Texas, and North Carolina,

and it has become the most important disease problem for many peanut growers (Culbreath et al. 1997a). Symptoms vary from severe stunting and distortion of peanut vines to elaborate concentric ring spots on individual leaflets, and in some cases, death of the entire plant. TSWV is vectored primarily by the thrip species *Frankliniella fusca* (Hinds) (tobacco thrips) and *F. occidentalis* (Pergande) (western flower thrips) in the United States, with tobacco thrips being the most important vector for secondary spread of TSWV (Lynch and Mack 1995). Because disease transmission is by intracellular feeders, there is no measure to cure the plant once it has become infected (Lynch and Mack 1995). Thrips concentrate in leaf terminals and flowers, which are areas that are protected from insecticide sprays (Wightman and Ranga Rao 1994). Small numbers of thrips can result in high rates of pathogen spread (Ullman et al. 1997), and because inoculation can occur quickly, pesticides do not kill the vector before they can transmit the virus. Because chemical controls are unavailable for the disease per se, the most important factor in management of spotted wilt is cultivar selection (Culbreath et al. 1999a).

Before the emergence of TSWV, 'Florunner' was the dominant cultivar in the Southeast peanut production area. However, 'Florunner' is highly susceptible to TSWV and yield is dramatically reduced (Culbreath et al. 1992a). Largely because of spotted wilt, there have been dramatic shifts in cultivars grown in Georgia, Florida, and Alabama (Culbreath et al. 2000) and 'Florunner' is no longer produced in this region. 'Southern Runner' was the first peanut cultivar observed with moderate levels of resistance to TSWV (Culbreath et al. 1992b, 1994, 1996). Intensive screening of cultivars and breeding lines has resulted in the release of several additional TSWV resistant cultivars, including 'Georgia Browne', 'Georgia Green' (Branch 1996), 'C-99R', and 'Florida MDR 98', all of which have a level of TSWV resistance similar to 'Southern Runner' (Culbreath et al. 1994, 1996, 1997b). Lyerly (2000) inoculated 'Georgia Green' and several *Arachis* species in greenhouse tests and observed that the cultivar was highly susceptible. She concluded that field resistance in 'Georgia Green' does not result from genetic resistance to the virus, but from a combination of other factors that suppress infection. Accessions of two diploid species (*A. diogoi* and *A. correntina* (Burkart) Krapov. and W. C. Gregory) were highly resistant to TSWV infection in greenhouse inoculation experiments (Lyerly 2000).

Unfortunately, none of the cultivars released to date has a high level of resistance to TSWV, and all available cultivars may suffer significant damage during extreme epidemics. The genetic mechanism responsible for resistance has not been elucidated. At the time TSWV emerged as a problem in the Southeast, PI 203396 was an ancestor to many breeding

populations due to its resistance to late leaf spot. Fortunately, PI 203396 also has resistance to TSWV, and was one parent of the TSWV-resistant runner-type cultivar 'Southern Runner'. PI 203396 is also in the pedigrees of the TSWV-resistant cultivars 'Georgia Green', 'Florida MDR98', and 'C-99R'. Other sources of resistance to TSWV are available in the U.S. *A. hypogaea* germplasm collection (Anderson et al. 1996a) as well as late generation breeding lines that have resistance equal to or better than currently available cultivars (Culbreath et al. 1999b).

Genetic engineering may also result in improved resistance because the nucleocapsid protein gene of TSWV has been inserted into peanut using microprojectile bombardment (Yang et al. 1998; Magbanua et al. 2000) and *Agrobacterium*-mediated transformation (Li et al. 1997). Progenies from transformation have shown protection against TSWV in the field (Li et al. 1997; Magbanua et al. 2000). However, this type of single gene resistance may be short-lived because there appears to be a highly heterogeneous natural viral population available for adaptation (Qiu and Moyer 1999). TSWV has a tripartite genome organization that allows potential exchange of information between related viral genomes (Qiu et al. 1998), and Qiu and Moyer (1999) demonstrated that genome reassortment is a genetic mechanism employed by this virus to adapt to resistant plants.

Because there is great interest by the peanut industry for production of cultivars with a high oleic acid concentration, the TSWV reactions to this germplasm deserves attention. The first peanut cultivars containing high oleic acid were extremely susceptible to TSWV (Culbreath et al. 1997b). Moderate levels of resistance to TSWV have been reported in the mid-oleic cultivars 'Florida MDR-98' (Culbreath et al. 1997b) and 'Viru-Gard' (Culbreath et al. 2000). High oleic breeding lines recently have been produced with acceptable levels of resistance to TSWV (Culbreath et al. 1999b).

5. Resistance to Preharvest Aflatoxin Contamination. *Aspergillus flavus* and *A. parasiticus* Speare can colonize seed of several agricultural crops including peanut (CAST 1989). This can result in the contamination of the edible yield from these crops with the toxic fungal metabolite aflatoxin. Elimination or suppression of preharvest aflatoxin contamination (PAC) in the food chain is one of the most serious challenges facing the U.S. peanut industry. Lamb and Sternitzke (2001) calculated that aflatoxin costs the farmer, buying point, and sheller segments of the southeast U.S. peanut industry over $25 million annually. Peanut genotypes with some resistance to invasion by *A. flavus* have been reported (Mehan et al. 1991; Cole et al. 1995). These genotypes were identified by screen-

ing germplasm using in vitro colonization by *A. flavus* of rehydrated sound mature kernels. Promising correlations between field resistance and in vitro resistance have been observed in Africa (Zambettakis et al. 1981; Waliyar et al. 1994) and India (Mehan et al. 1986, 1987). However, this in vitro screening has produced inconsistent results when compared to a natural field situation in the United States where Anderson et al. (1995) and Blankenship et al. (1985) did not observe significant levels of preharvest aflatoxin resistance in genotypes previously reported with in vitro resistance; and Kisyombe et al. (1985) observed significant field resistance in only one of 14 in vitro resistant selections.

These initial screening efforts for resistance to preharvest infection and aflatoxin contamination were hampered by a lack of basic knowledge about the fungus and by technological limitations in measuring resistant reactions. Since these early efforts, much information has been gathered about the influence of environmental stress on aflatoxin contamination in peanuts. Detailed studies on the effect of temperature and moisture stress on colonization of kernels and aflatoxin contamination of peanuts have been conducted (Cole et al. 1982; Hill et al. 1983; Sanders et al. 1985). Technological advances also have provided great improvement in detection and measuring techniques for assessing aflatoxin contamination (Wilson 1989) which can more accurately measure resistance in a field or greenhouse environment (Holbrook et al. 1994; Anderson et al. 1996b; Holbrook et al. 1998c).

Holbrook et al. (1994) developed a large-scale field screening technique to directly measure field resistance to PAC that uses subsurface irrigation in a desert environment to allow an extended period of drought stress in the pod zone while keeping the plant alive. Without subsurface irrigation, peanut plants died and their seeds rapidly dehydrated in the soil before contamination could occur. Sanders et al. (1993) also observed high levels of aflatoxin contamination when peanuts in the pod zone were artificially stressed with heat and drought while keeping plants nonstressed by providing root zone irrigation. Large-scale field screening for resistance to PAC was also enhanced by the development of a consistently successful and reproducible field inoculation technique (Will et al. 1994). Artificial inoculation helps to insure uniform testing conditions, which reduces variation due to escapes that often masks genetic differences. Anderson et al. (1996b) developed a screening technique that can be used in greenhouse facilities where high amounts of preharvest aflatoxin accumulation were produced by completely isolating the pod zone and restricting moisture to the root zone. Because aflatoxin concentrations are higher when the plant is stressed, development of cultivars with reduced aflatoxin contamination

when grown under heat- and/or drought-stressed conditions would be a valuable tool in alleviating this problem.

Screening of the U.S. peanut core collection (Holbrook et al. 1993) resulted in the identification of 15 accessions that showed low levels of aflatoxin contamination in multiple environments (Holbrook et al. 1998c). These accessions exhibited a 70 to 90 percent reduction in aflatoxin contamination in comparison to susceptible accessions in at least three environments.

Development of resistant cultivars could be accelerated if an effective trait for indirect selection can be identified. Holbrook et al. (1997) conducted a study to determine if resistance to other fungi could be used as an indirect selection tool for resistance to colonization of peanut by *A. flavus* and/or aflatoxin contamination. Genotypes with resistance to late leaf spot and/or white mold were evaluated, but none exhibited less *A. flavus* colonization or aflatoxin contamination than 'Florunner'. These results indicate that the mechanisms of resistance to these two fungi did not effect colonization by *A. flavus* or aflatoxin production.

Drought tolerance is another characteristic that has the potential to serve as an indirect selection tool for resistance to PAC. Holbrook et al. (2000a) evaluated the resistance to PAC in genotypes that had varying levels of drought tolerance (Rucker et al. 1995) and concluded that tolerant genotypes also had greatly reduced aflatoxin contamination. Significant positive correlations were observed between aflatoxin contamination and leaf temperature and between aflatoxin contamination and visual stress ratings. A significant negative correlation was also observed between aflatoxin contamination and yield under drought stressed conditions. Leaf temperature, visual stress ratings, and yield are all less variable and relatively inexpensive to measure compared to the amount of aflatoxin in seed samples. A similar relationship between drought tolerance and reduced aflatoxin contamination was observed in the drought tolerant cultivar 'Streeton' in Australia (Cruickshank et al. 2000). This cultivar has up to 40 percent lower aflatoxin levels during years of high aflatoxin incidence in comparison to other cultivars. Physiological studies (Nageswara Rao et al. 2000b) have shown that the lower aflatoxin incidence is associated with better root water uptake resulting in better maintenance of crop water status during severe end-of-season drought.

Several in vitro studies have indicated that fatty acid composition could either directly or indirectly affect aflatoxin contamination (Fabbri et al. 1983; Passi et al. 1984; Doehlert et al. 1993; Burow et al. 1997a). Holbrook et al. (2000e) evaluated the effect of altered fatty acid composition on PAC in peanut, but observed no measurable effect of reduced

linoleic acid composition on PAC. They concluded that the products of the lipoxygenase pathway that have been shown to affect aflatoxin biosynthesis in vitro may not be present in sufficient quantities to effect aflatoxin contamination of developing peanut seed.

6. Improved Drought Tolerance. The peanut plant is highly drought-tolerant and is grown in many areas of the world where most other food legumes will not produce a crop. However, insufficient water at the time of flowering and fruiting will significantly reduce yield. Further, aflatoxin contamination is mainly a problem in peanut that has been sub-jected to heat and drought stresses late in the growing season (Sanders et al. 1985). The issues surrounding agricultural water use are increas-ing in importance, and the development of cultivars with improved drought tolerance should help alleviate these concerns.

Drought tolerance may be enhanced by improvements in soil water extraction capability (Wright and Nageswara Rao 1994), or improvements in water use efficiency, or both (Hebbar et al. 1994). Rucker et al. (1995) evaluated drought tolerance characteristics of 19 peanut genotypes which differed in the size of their root systems. Under drought-stressed field conditions, these genotypes differed in canopy temperature and visual stress ratings, two potential measures of drought tolerance. Wright et al. (1994) demonstrated genetic differences in peanut for transpiration effi-ciency which is defined as g of dry matter produced per kg of water tran-spired. Measurements of transpiration and/or root biomass are difficult and therefore are not practical for use in large scale breeding efforts for improved drought tolerance.

Farquhar et al. (1982) proposed that the transpiration efficiency of a genotype could be estimated by measuring the carbon isotope discrim-ination (Δ) in leaves. Transpiration efficiency in peanut genotypes is neg-atively correlated (r ranging from –0.88 to –0.92, P < 0.01) with Δ (Hubick et al. 1986, 1988; Wright et al. 1988, 1994). While measurement of Δ is rapid, it is an expensive measurement and may not be applicable to large segregating breeding populations.

Specific leaf area (ratio of leaf area to leaf dry weight) also is highly correlated with Δ in peanut (Nageswara Rao and Wright 1994). Specific leaf area can be easily and inexpensively measured, and it is being used in a large-scale screening program for improved drought resistance in Australia (Nageswara Rao et al. 2000a). This research group has demon-strated progress from using physiological traits to indirectly select for high-pod yield of peanut under water-limited conditions. After two cycles of selection, they selected progenies that yield 30 percent more than their parents under drought-stressed conditions (Nageswara Rao et

al. 2000b). However, care must be taken when using specific leaf area as a selection criteria since it is significantly influenced by time of sampling and leaf age (Wright and Hammer 1994; Nageswara Rao et al. 1995). Wright et al. (1996) observed variation in the strength of correlations between specific leaf area and Δ in a range of peanut genotypes and environments.

Nageswara Rao et al. (2001) evaluated the use of a hand-held portable SPAD chlorophyll meter for rapidly assessing drought tolerance in peanut. They observed a significant correlation ($r = 0.77$, $P < 0.01$) between the chlorophyll meter reading and specific leaf area and suggested that this meter could be used as a rapid and reliable measure to identify genotypes with low SLA, and hence high transpiration efficiency in peanut.

7. Improved Oil Quality. Properties of peanut oil are determined by the fatty acid composition. Two fatty acids, oleic (O) and linoleic (L), comprise over 80 percent of the oil content of peanut. Standard peanut cultivars average 55 percent oleic acid and 25 percent linoleic acid (Knauft et al. 1993). Linoleic acid is less saturated and less stable than oleic acid, and the oxidative stability and shelf life of peanut and peanut products can be enhanced by increasing the O/L ratio. Norden et al. (1987) examined the fatty acid composition of 494 genotypes and identified two breeding lines with 80 percent oleic acid and 2 percent linoleic acid. This was a major deviation from previously known levels of fatty acid composition in peanut.

Moore and Knauft (1989) found that inheritance of the high-oleate trait was controlled by duplicate recessive genes, ol_1 and ol_2. F435 differed at both loci from a virginia-type line but at only one locus from a runner line. Knauft et al. (1993) reported monogenic inheritance in crosses of the runner market-type cultivars and breeding lines. A cross with a virginia market-type segregated in a 15:1 ratio typical of recessive digenic inheritance. The authors concluded that one of the recessive alleles occurs with high frequency in peanut breeding populations in the United States whereas the other allele is rarer. Isleib et al. (1996) examined five different cultivars of virginia-type peanut cultivars and found that four were either $Ol_1Ol_1ol_2ol_2$ or $ol_1ol_1Ol_2Ol_2$ and one was $Ol_1Ol_1Ol_2Ol_2$. When only one gene transfer is required, Isleib et al. (1998) were able to identify heterozygotes based on linoleate levels. This will allow breeders to identify carriers of the recessive allele in successive cycles of backcrossing without intervening generations of selfing and decrease the time required to achieve the desired number of backcrosses. Lopez et al. (2001) examined the inheritance of high oleic acid in six

spanish market-type peanut cultivars. Segregation patterns indicated that two major genes were involved. However, the presence of low-intermediate O/L ratio genotypes indicated that other genetic modifiers might be involved in the expression of the O/L ratio in these genotypes. Isleib et al. (1998) also observed an effect of other loci on fatty acid concentrations. Studies of peanut lines without the high oleic characteristic have indicated that oleic content can be influenced by additive gene effects (Mercer et al. 1990), and by additive × additive epistasis (Upadhyaya and Nigam 1999).

Gorbet and Knauft (1997) found that 'SunOleic 95R', a high oleic runner cultivar, had a much longer shelf life than the traditional runner-type peanut cultivars. Peanuts with high levels of oleic acid also show some promise for beneficial health effects in humans and animals that consume them.

8. Improved Flavor. Flavor of roasted peanuts is an essential characteristic influencing consumer acceptance, and enhancement of roasted peanut flavor is an important objective of the peanut industry. Only recently has it been recognized that the roasted peanut attribute is an inherited trait (Sanders et al. 1995). Through the research of Pattee and coworkers, several roasted peanut quality sensory attributes have been shown to be heritable (Pattee and Giesbrecht 1990; Pattee et al. 1993, 1995a, 1998; Isleib et al. 1995b).

Isleib et al. (2000) examined the genotypic variation in roasted peanut flavor quality in breeding lines and cultivars developed since 1930. They concluded that the negative influence of commonly used ancestors in virginia-type cultivars has resulted in trends toward poorer roasted peanut flavor (reduced intensity of the roasted peanut and sweet attributes and increased intensity of the bitter attribute). Conversely, runner and spanish types tend to give better roasted peanut flavors. After estimating the ancestral contribution to roasted peanut flavor for 128 cultivars and breeding lines, Isleib et al. (1995b) concluded that the parental line 'Jenkins Jumbo' (Hammons and Norden 1979) was the single most important ancestor in virginia-type peanuts, and this ancestor exerted a highly negative effect on flavor. 'Jenkins Jumbo' was initially used as a source of large pod and seed size without the knowledge that it would have a deleterious effect on flavor. Isleib et al. (1995a) also reported that at least one parent commonly used as a source of disease resistance (PI 203396) can reduce the roasted flavor of its progeny. Pattee et al. (2001) reported that the three peanut cultivars with resistance to CBR have a negative effect on flavor in progenies. They urged caution when incorporating exotic germplasm into breeding populations, and suggested

flavor evaluations as soon as practical in the breeding process. Over the same time period, runner-type cultivars have increased slightly in average sweetness; however, there has been an increase in the variance of roasted peanut intensity in breeding populations since 1980.

Best linear unbiased prediction (BLUP) is a method for predicting the breeding value of a parent based on the performance of its relatives (Henderson 1975). Pattee et al. (2001) concluded that BLUPs of breeding value can be used to predict cross means, but segregation within crosses provides additional opportunity for progress from selection. BLUPs of breeding values were superior to midparent values in predicting cross means. These authors identified large-seeded lines with superior flavor, indicating that it should be possible to improve flavor in the virginia market-type without sacrificing large seed size.

Pattee and Knauft (1995) evaluated four high oleic acid breeding lines and observed no changes in roasted peanut attribute intensity in comparison to 'Florunner'. Pattee et al. (2001) observed that high-oleic cultivars and breeding lines derived by backcrossing with 'Sunrunner' (Norden et al. 1985) had a high positive breeding value for the roasted peanut attribute. It is not clear if this is a real genetic effect or an artifact of the sensory evaluation since the protocol requires a storage period during which some oxidation of linoleic acid in the 'Sunrunner' seeds may occur that could produce off-favors.

Cultural preferences should influence breeding decisions about flavor. Local consumers in some areas of Mexico have a distinct preference for the flavor characteristics of *A. hypogaea* spp. *hypogaea* var. *hirsuta* (Becker 1993). However, these *hirsuta* accessions did not have a higher intensity of the roasted peanut attributes that are favored in the United States (Pattee et al. 1995b). Some of the *hirsuta* landraces did have a higher intensity of sweetness that may account for their preference in some parts of Mexico.

9. Breeding for Allergen Resistance. Peanut allergens cause severe reactions in approximately 0.6 percent of the population in the United States, and exposure can be fatal even with exposure to trace amounts of peanut protein. Thus, allergens are of great concern to the peanut scientific community and a highly desirable objective would be to develop nonallergenic peanut cultivars. Several proteins related to seed storage protein complex are responsible for causing allergic reactions, with Ara h 1 and Ara h 2 being the major contributors. Although serology of the peanut allergy appears to be different in regions of the world, Koppelman et al. (2001) did not find differences among genotypes. Thus, traditional breeding methodologies will not solve the problem until variation

is identified in the species. Research efforts are being placed into developing vaccines to peanut allergens as opposed to developing plant breeding programs.

B. Marker-Assisted Selection

Isozyme analyses of cultivated peanut have shown little variation (Grieshammer and Wynne 1990), but polymorphisms are somewhat more frequent between interspecific hybrids (Lacks and Stalker 1993). Isozyme studies of species in section *Erectoides* showed a large amount of variation, and species appeared to associate with members of other sections. These observations were clarified when Krapovickas and Gregory (1994) divided the *Erectoides* into three sections (*Erectoides, Trierectoides,* and *Procumbentes*). Analyses of seed storage proteins have shown that variation exists among species of section *Arachis* (Singh et al. 1991a; Bianchi-Hall et al. 1993, 1994), but proteins are not useful for descriptions at the species level.

Restriction fragment length polymorphisms (RFLP) represented the first marker system that has a sufficiently large number of polymorphisms that could be used to create linkage maps and to implement indirect selection strategies. In *A. hypogaea*, little molecular variation has been detected by using RFLP technologies (Kochert et al. 1991). However, significant amounts of variation for RFLP (Kochert et al. 1991; Paik-Ro et al. 1992) and polymerase chain reaction (PCR) (Halward et al. 1992, 1993) have been observed among *Arachis* species. Accessions in section *Arachis*, representing taxa that will hybridize with *A. hypogaea*, have been analyzed using RFLPs and then multivariate analysis has been used to group accessions into clusters (Kochert et al. 1991) that corresponded closely with morphological traits (Stalker 1990). Tetraploids were clearly separated from diploids in both investigations. Stalker et al. (1995a) utilized RFLPs to examine genetic diversity among 18 accessions of *A. duranensis* Krapov. & W. C. Gregory, and they found more variation between than within accessions; and individual accessions could be identified. Kochert et al. (1996) concluded that the cultivated peanut originated from a cross between *A. duranensis* and *A. ipaensis*. Chloroplast analysis indicated that *A. duranensis* was the female progenitor of the cross (Kochert et al. 1996).

An RFLP map was developed for peanut by analyzing an F_2 population from the diploid ($2n = 2x = 20$) interspecific cross *A. stenosperma* (acc. HLK 410) and *A. cardenasii* (acc. GKP 10017). The linkage map covered 1063 cM with 117 markers in 11 linkage groups. Fifteen unassociated markers were also reported (Halward et al. 1993). A second

molecular map of peanut has been created by using a tetraploid cross of cultivar 'Florunner' × 4*x* {*A. batizocoi* (acc. GKP 9484) × [*A. cardenasii* (acc. GKP 10017) × *A. diogoi* (acc. GKP 10602)]} (M. D. Burow, pers. comm.) where more than 380 RFLP markers have been mapped. Most markers had disomic inheritance, with the exception of one linkage group that may be polysomic. Further, the R239 marker for nematode resistance maps to the same linkage group on both the maps produced by Halward et al. (1993) and Burow, Patterson, and Simpson (M. D. Burow, pers. comm.). Garcia (1995) used RAPDs to add markers to the map and found coliniarity between RAPDs and RFLPs.

Garcia et al. (1996) used RAPD and sequence characterized amplified regions (SCARs) technologies to map two dominant genes conferring resistance to the peanut root-knot nematode *M. arenaria* race 1. In their study, the cultivated peanut was crossed with a tetraploid breeding line that had a resistant species [*A. cardenasii* (GKP 10017)] in the pedigree. Bulked segregant analysis was used to find RAPD markers common to both resistant progeny and the resistant *Arachis* species. One marker (Z3/265) was closely linked with *M. arenaria* resistance and subsequently mapped to a linkage group on a backcross map in an area known to contain *A. cardenasii* introgression. This fragment was cloned to make SCAR and RFLP probes, and linkages confirmed (Garcia et al. 1996). Burow et al. (1996) also linked RFLP markers to genes conditioning *M. arenaria* resistance in the tetraploid cross of cultivar 'Florunner' × 4x [*A. batizocoi* (*A. cardenasii* × *A. diogoi*)], but it is not known whether the genes identified in the two crosses are the same.

In an investigation to link molecular markers with resistance to *C. arachidicola,* Stalker and Mozingo (2001) reported associations of RAPDs with a gene conferring resistance to sporulation, lesion diameter, defoliation, and overall rating in an interspecific hybrid with *A. cardenasii* in the pedigree. A marker also was associated with resistance to southern corn rootworm damage. The resistance genes likely originated from the wild species parent. In addition, they associated markers with Cylindrocladium black rot resistance and sporulation to *C. arachidicola* in a cross between cultivar 'NC 7' (Wynne et al. 1979) and PI 109839. This represented the first report of molecular markers being associated with resistance genes in an *A. hypogaea* × *A. hypogaea* cross.

He and Prakash (1997) were the first investigators to report applications of amplified fragment length polymorphisms (AFLP) technologies in peanut. They used 28 primer pairs to generate 111 AFLP markers in *A. hypogaea.* They reported a greater amount of variation using this technology than with any other molecular marker technique. However, other studies conducted with cultivated peanut have shown less varia-

tion than reported by He and Prakash using this technology (Mila and Stalker, unpublished data). Simple sequence repeats (SSR) markers are highly variable, codominant, easily detected from relatively little amounts of DNA after PCR amplification, and reportedly more variable than other marker systems. Hopkins et al. (1999) reported six polymorphic SSRs in *A. hypogaea* with the number of fragments amplified per SSR ranging from 2 to 14. Newer technologies commonly used in other legumes such as Medicago species have not been published in the peanut literature, in large part because few programs are currently working in the area of molecular marker expression using *Arachis* species.

C. Interspecific Hybridization

Creating hybrids among *Arachis* species is difficult, but the high levels of resistance to the many diseases and insect pests that plague peanut have generated much interest in recovering interspecific hybrids. Although transformation technologies are alternatives for utilizing resistant species that will not hybridize with *A. hypogaea,* genes or gene complexes that confer high levels of disease or insect resistance have not been isolated in peanut. Until agronomically useful genes are isolated and shown to be stably expressed by transformation technologies, interspecific hybridization is the most promising method to introgress genes from related *Arachis* species that are not present in the cultivated peanut.

The most comprehensive crossing study in peanut was completed by Gregory and Gregory (1979), who set up a diallel crossing program with 100 accession of *Arachis* species. Their work indicates that crosses between species of different sections result in very few hybrids, and all progenies are sterile. Hybrids within sectional groups are easier to produce and fertility levels are generally higher, although a considerable amount of sterility can still occur (Stalker et al. 1991b). Bridge crosses have also been attempted with species in sections *Rhizomatosae* and *Erectoides,* but Stalker (1985a) concluded that the germplasm outside section *Arachis* is inaccessible to the domesticated peanut through sexual hybridization.

Restricted fertilization is not believed to be the cause of hybridization failures in most interspecific peanut crosses (Sastri and Moss 1982). However, application of gibberellic acid or mentor pollen to the stigma at the time of pollination may increase the frequency of pegging (Sastri and Moss 1982; Stalker et al. 1987). Using annual species as female parents versus perennial species usually results in a higher success rate, which may be related to perennials having smaller stigmas and being

surrounded by a protective ring of hairs (Lu et al. 1990). Because of the apparent immunity of species in section *Rhizomatosae* to leaf spots and many viruses, research programs in the United States prior to 1980 (as well as much of the work at ICRISAT since that time) have concentrated on introgressing genes from *A. glabrata* into *A. hypogaea*. However, only species in section *Arachis* are readily available for gene introgression, so this part of the chapter will concentrate on interspecific hybrids with species in the primary (*A. hypogaea* and *A. monticola*) and secondary (diploid species in section *Arachis*) gene pools.

Arachis hypogaea × *A. monticola* hybrids are relatively easy to produce and the taxa represent one biological species. Most of the diseases and insects that are problematic in the domesticated species are also a problem with *A. monticola,* and considering that *A. monticola* has fragile pegs and one-seeded pods, it has generally not been considered as a good parent for crop improvement. Further, hybrids many times have prolonged dormancy (Stalker and Simpson 1995), which hinders breeding progress. However, two cultivars have been released with *A. monticola* in their pedigree (Hammons 1970; Simpson and Smith 1975), but neither has been produced on large areas.

Diploid species of section *Arachis* have greater potential for cultivar improvement than *A. monticola* because many accessions have very high levels of resistance to many economically important insect pests (Stalker and Campbell 1983; Lynch and Mack 1995) and diseases (Stalker and Moss 1987; Stalker and Simpson 1995). Several methods have been attempted to introgress germplasm into *A. hypogaea* from diploid species with each having advantages and disadvantages; but none of them lead to quick introgression of desired genes because of sterility in progenies and limited genetic recombination. However, several species contain traits not found at high levels in *A. hypogaea* [e.g., TSWV resistance in *A. diogoi* and *A. correntina* accessions (Lyerly 2000)], and the efforts involved in producing interspecific hybrids can be rewarding.

Introgression of useful genes into *A. hypogaea* is not a trivial exercise even when cross-compatible species are used because sterility barriers are present due to different ploidy levels, genomic incompatibilities, and cryptic genetic differences. Constraints to obtaining hybrids may occur at the time of fertilization, during early cell division of the embryo, because the embryo does not reinitiate growth after a quiescent phase during peg elongation, or during later embryo development. Even when hybrids are obtained, genetic recombination is often restricted, and desired genes are not incorporated into the *A. hypogaea* genome. Thus, simply obtaining fertile and stable 40-chromosome progenies from inter-

specific hybridization does not guarantee gene incorporation into the desired genome. Introgression of useful traits in peanut is a two-step process where a trait is first incorporated into the *A. hypogaea* genome (which also results in progenies with many unfavorable traits), and then a plant breeding program is initiated to enhance yield and quality traits while at the same time selecting for the desired trait.

Direct crosses with *A. hypogaea* have been obtained with both A and B genome species of section *Arachis*. Krapovickas and Rigoini (1951) produced the first interspecific hybrid with *A. villosa* var. *correntina,* and since then many other interspecific combinations have been successful (Stalker and Moss 1987; Stalker and Simpson 1995). Although most of the diploid species hybridize relatively easily with the domesticated peanut, several interspecific hybrids are difficult to obtain (Stalker et al. 1991b). When the domesticated species is used as the female parent, hybridization is usually more successful. Direct hybridization between *A. hypogaea* and diploids results in sterile triploid hybrids. Fertility can be restored at the hexaploid level after colchicine treating vegetative cuttings (Singh et al. 1991b), or sometimes by simply propagating plants under field conditions for prolonged periods of time in a frost-free environment (Singh and Moss 1984). Hexaploids are expected to have 30 bivalents, but many plants are cytologically unstable and have up to 30 univalents (Company et al. 1982). Thus, most hexaploids produce very few seeds. Hexaploid × diploid (and reciprocal) crosses abort, so a one-step program to lower the chromosome number to the tetraploid level is not possible (Halward and Stalker 1987b). Reducing the chromosome number to $2n = 40$ has been accomplished by several methods, including self-pollination and subsequent chromosome loss (Stalker 1992) and by backcrossing with *A. hypogaea*. When hexaploids are backcrossed with the tetraploid *A. hypogaea,* pentaploids result that are mostly sterile and produce few flowers, and continued backcrossing is not a practical breeding strategy. Unexpectedly, some pentaploids have 25 bivalents (Company et al. 1982) which indicates that there is more genomic similarity between *A. hypogaea* and related diploid species than the commonly designated A and B genomic designations would indicate. When pentaploid plants are allowed to self-pollinate, a few will produce viable aneuploid progenies and a second generation of selfing will usually result in tetraploid progenies from which fertile lines can be selected.

Garcia (1995) investigated introgression of genes from diploid *Arachis* species to *A. hypogaea* by crossing the cultivated peanut with several diploid species, restoring fertility after colchicine treating F_1s to produce fertile hexaploids, and then selfing hexaploids and backcrossing with a

recurrent parent at each respective generation after selfing. Garcia found that increasing numbers of molecular markers were lost during each self-ing generation, which likely resulted from meiotic irregularities and subsequent random loss of genes. Garcia et al. (1995) also analyzed a tetraploid population derived by selfing hexaploids and reported intro-gression of *A. cardenasii* (A genome species) genes into *A. hypogaea* in 10 of the 11 linkage groups on a molecular map. The authors concluded that this was evidence that the genomes of *A. hypogaea* are similar and that the species is not a true allopolyploid. Progenies selected from the highly diverse *A. hypogaea* × *A. cardenasii* population were highly resistant to early leaf spot caused by *C. arachidicola,* late leaf spot caused by *C. personatum,* peanut root-knot nematode, southern corn rootworm (*Diabrotica undecimpunctata howardi* Barber), and potato leafhopper (*Empoasca fabae* Harris). Several germplasm lines have been released from these progenies (Stalker and Beute 1993; Moss et al. 1997; Stalker et al. 2002a,b; Stalker and Lynch 2002).

A second method to produce tetraploid interspecific hybrids is to produce autotetraploids or amphiploids of *Arachis* species prior to crossing with *A. hypogaea.* Polyploids are relatively easy to produce in peanut by colchicine-treating germinating seeds, but cytological identi-fication of polyploid branches is necessary to confirm chromosome numbers of reproductive tissues. Autotetraploids have been produced with at least eight diploid species of section *Arachis* (Singh 1986a), but they are generally weak plants and do not survive for more than one growing season. Thus, crossing programs between autotetraploids and *A. hypogaea* need to be conducted as soon as plants are cytologically identified. Germplasm lines have not been released from this cytologi-cal pathway in peanut.

Amphidiploids can also be produced between two or more diploid species before crossing with *A. hypogaea.* Gardner and Stalker (1983) created amphidiploids of hybrids between A-genome diploids and observed high bivalent association in the F_1 hybrids with *A. hypogaea.* When amphidiploids are created by crossing *A. batizocoi* (B genome) with A-genome species, there are usually a greater numbers of bivalents in the polyploids. Although advantages exist for using *A. batizocoi* as a parent in crosses to enhance fertility restoration, this species is suscep-tible to late leaf spot and other diseases, which may result in unfavor-able traits being introduced into breeding lines. Rust-resistant hybrids have been selected from progenies of *A. hypogaea* × amphiploid (*A. bati-zocoi* × *A. duranensis*) and (*A. correntina* × *A. batizocoi*) (Singh 1986b). Simpson et al. (1993a) released a germplasm line derived from a 4*x* [*A. batizocoi* (*A. cardenasii* × *A. diogoi*)] cross as well as its backcross with

'Florunner'. Both germplasm lines were highly resistant to the root-knot nematode, *M. arenaria.* Simpson and Starr (2001) also released the cultivar 'COAN', a backcross of this amphiploid to the cultivar 'Florunner' that is resistant to *M. arenaria* and *M. javanica.*

D. Transgenic Technology

The only viable alternative for accessing genes in the tertiary gene pool (or ones outside the genus) is to insert genes using transformation techniques. Utilizing this technology first depends on having a reliable tissue culture system to regenerate plants. In peanut, research was conducted for several decades by many investigators to develop reliable plant regeneration systems. The first successful in vitro system for regeneration in peanut was with deembryonated cotyledons (Illingsworth 1968). Although regeneration is highly influenced by genotype, media, light, temperature, and growth regulators, shoots have now been obtained from peanut using several explants and dedifferentiated callus cultures (Ozias-Akins and Gill 2001). Young leaflets can be used for regeneration, but only cells surrounding the central vein will produce callus that is competent for plant regeneration (Cheng et al. 1992; Utomo et al. 1996; Akasaka et al. 2000). These types of cells are susceptible to *Agrobacterium* infection but to date, only the genotype 'New Mexico Valencia A' has been shown to be capable of regeneration after *Agrobacterium* infection (Cheng et al. 1994, 1996). Protoplasts have only been regenerated from cells derived from immature cotyledons (Li et al. 1995). Ozias-Akins and Gill (2001) indicated that stable transformation using other genotypes has been incompletely documented, and they concluded that *Agrobacterium* transformation has restricted value for improving cultivated peanut.

Many tissue types can now be regenerated in vitro, including hypocotyls, immature leaflets, leaf sections, cotyledons, and epicotyls. Because actively dividing cells are required to integrate foreign DNA into tissues, embryogenic cultures that divide rapidly are highly desirable, and cotyledons or immature embryos are good sources of callus for transformation in peanut (Ozias-Akins et al. 1992, 1993; Baker and Wetzstein 1995). Because researchers have been interested in developing cultivars adapted to specific geographic regions, many genotypes have been tested, and Ozias-Akins and Gill (2001) summarized the tissue culture protocols and genotypes used in peanut. Transformation techniques can be applied to primary cultures if shoot primordia or somatic embryos are formed directly from an explant, from dedifferentiated callus cultures, or repetitive tissue cultures. Suspension cultures are more

difficult to use in peanut than cultures on semi-solid medium because recovery of fertile plants is difficult and genotype dependent (Ozias-Akins and Gill 2001).

Tissue electroporation has not been reported in *A. hypogaea* (Ozias-Akins and Gill 2001), and microprojectile bombardment has been the most consistent and successful transformation technique in the species. Although transient expression can be used to monitor gene incorporation, it does not always correlate with gene transfer (Altpeter et al. 1996). Thus, selectable markers are usually used to identify transformed cells or tissues. Hygromycin phosphotransferase and neomycin phosphotransferase II are the most frequently used for antibiotic selection in peanut.

Gene promoters are the most critical element for obtaining gene expression in peanut, and several work in peanut, including ones derived from monocots and dicots (Ozias-Akins and Gill 2001). The CaMV35S promoter is the most commonly used promotor in peanut and the only one used to control the *hph* gene (Ozias-Akins and Gill 2001). Genes have been inserted into *A. hypogaea* for virus (Brar et al. 1994; Li et al. 1997; Yang et al. 1998; Magbanua et al. 2000; Sharma and Anjaiah 2000) and lesser cornstalk borer resistances (Singsit et al. 1997). Durable resistance to tomato spotted wilt viruses is yet to be achieved (Li et al. 1997; Magbanua et al. 2000), but introduction of the crystaline proteins from *Bacillus thuringensis* appear to be stable (Ozias-Akins and Gill 2001). The later transformation system was developed more to reduce aflatoxin contamination in peanut than to inhibit the lesser cornstalk borer.

Many potentially important traits could be incorporated into the cultivated genome, and transformation technologies will become increasingly important for peanut breeding as genes are isolated with agronomic potential. Especially important will be genes conditioning disease resistance and seed quality, however, no transgenic peanuts are currently in the marketplace.

VII. SUMMARY

A large effort has been made to collect and preserve genetic resources in both *A. hypogaea* and related *Arachis* species. Although additional collecting is needed in South and Central America, the germplasm collection is large and represents a significant part of the variation in the genus. International germplasm exchange has become problematic during recent years, not because of individuals in the scientific community, but because of political constraints on collection and distribution of seeds. Creating a peanut core collection has greatly enhanced evaluation

research in peanut during recent years, and sources of resistance to many pests of peanut have been identified.

Most major peanut-producing states employ peanut breeders but to date, cultivars originating from Florida, Georgia, North Carolina, and Texas have dominated the peanut hectarage. Only one private company and one U.S. Department of Agriculture scientist are involved in peanut cultivar development. Plant breeding efforts in peanut have shifted emphasis during recent years from mostly selecting for increased yields to also selecting high-yielding cultivars with greater resistance to biotic stresses and enhanced quality traits, especially for improving oil profiles and flavor characteristics. The prevalence of foliar and soilborne diseases continues to keep peanut yields well below their potential levels, and until diseases such as TSWV, sclerotinia blight, and white mold can be suppressed, average yields will likely not increase. If the federal peanut support program changes to further reduce or eliminate price supports for peanut, then there will be greatly increased emphasis on lowering production costs while increasing biotic stress resistances in future cultivars. Cultivars with multiple sources of high levels of pest resistance will be needed in the future, an endeavor that has been very difficult for this crop species. In addition, breeding for drought resistance is a high priority set by the producer who wishes to maximize yields and for the manufacturer who needs a product free from aflatoxins.

Although cultivar development has traditionally emphasized improvement of *A. hypogaea* genotypes through pedigree selection, interspecific hybridization has received much attention since the 1960s in large part because of the high levels of pest resistances identified in wild peanut species. Genetic resistance to several of the most important pathogens of peanut, including TSWV, have only been found in species related to *A. hypogaea.* The first peanut cultivar with a diploid wild species in its pedigree was recently released for commercial production, and others should follow within a few years.

Molecular technologies are being developed for peanut, but little detectable molecular variation exists in *A. hypogaea.* However, a large amount of molecular variation is present in species of *Arachis,* and marker-assisted selection has great potential for enhancing introgression of useful traits from related species to cultivars. Transgenic technologies have been developed to insert foreign genes into the cultivated peanut, and the critical component needed for cultivar development is identification of agronomically useful genes. Cultivars developed with transgenic technologies have not been released for production, but several programs are working toward this goal. Regardless of the methodologies used in the future, critical needs are to lower production costs by selecting for abi-

otic stress resistances, to select genotypes that will increase consumer safety by lowering toxin levels in the seed, and to create higher consumer demands for peanut products through enhanced quality factors.

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